

16. On the External Characters of *Elaphurus*, *Hydropotes*,
Pudu, and other Cervidæ. By R. I. ПОСОК, F.R.S.

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(Text-figures 2-17.)

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Introduction.

In a paper "On the Specialised Cutaneous Glands of Ruminants" (P. Z. S. 1910, pp. 840-986) I described in some detail these glands in a considerable number of genera and species of Cervidæ, pp. 939 to 967 of the memoir being devoted to this family. Several well-marked forms, however, were not at that time available for examination, *Elaphurus*, *Hydropotes*, and *Pudu* being three of the most important. Since that time examples of *Elaphurus* and *Pudu*, exhibited in the Zoological Gardens, came after death into my hands in the Society's Prosectorium; and the Duke of Bedford, knowing my interest in the subject, very kindly sent to me from Woburn the body of a freshly-killed male example of *Hydropotes*. I am also greatly indebted to His Grace for the chance to examine a second specimen of *Elaphurus*, the body of which he was good enough to send to me. I must also take this opportunity of thanking Major A. Pam, O.B.E., for securing for the Society at my special request the example of the *Pudu* on one of his trips to Chili. To the subjoined account of the external characters of these three rare and isolated genera of Cervidæ, I have added descriptions of some less interesting species which I had not actually examined previously, although the characters of related species belonging to the same genera had been recorded by me. The following paper therefore is supplementary to the one I published in 1910. To facilitate comparison between the two papers, I have in the following pages quoted after each specific heading the page in my previous memoir where the genus or species was referred to.

I have also included in this paper some notes on the rhinarium, ears, facial vibrissæ, and penis, which I did not describe in 1910.

Finally, I must express my regret that, when writing on the glands in 1910, I inadvertently omitted to consult and quote Caton's valuable work on the deer of North America. In this he fully described the glands and other external characters of the species of that country, including those now known as *Rangifer tarandus*, *Alces alces*, *Odocoileus virginianus*, *O. columbianus*, *O. hemionus*, and *O. acapulcensis*, the last-mentioned being regarded at the present time as a subspecies of *O. virginianus*.

To Caton also we owe, I believe, the discovery of the very remarkable fact that in *Odocoileus* the sheath of the penis, instead of being confluent with the skin of the abdomen, so that the short prepuce is situated about halfway between the groin and the umbilicus, is long, pendulous, quite free from the skin of the groin, except at its base, which is close to that of the scrotum.

Genus CERVUS Linn.

CERVUS ELAPHUS Linn. (p. 941).

The feet and glands of a second specimen are identical with those described in 1910.

The rhinarium has the infranarial portion mesially sulcate and slightly narrower than the area between the nostrils; it is not, however, visible in profile view, owing to the forward extension of the hairs of the upper lip. On the upperside the hairs of the muzzle eneroach in the middle line some distance beyond the posterior angle of the nostrils. The buccal and ocular vibrissae are well developed; the interramal tuft is represented by a single vibrissa and the genal tuft by two placed close together and set halfway between the line of the mouth and of the eye, beneath the posterior angle of the latter.

CERVUS CANADENSIS Erxl.

The rhinarium resembles tolerably closely that of *C. elaphus*, except that the upper surface is more overgrown with hair, which extends nearly as far as the anterior border of the nostrils, and the infranarial portion is also narrower, being much narrower than the area between the nostrils, owing to the forward and inward extension of the hairs of the upper lip. (Text-fig. 2, A, B.)

The Asiatic Wapiti (*Cervus xanthopygus*) has a very similar rhinarium.

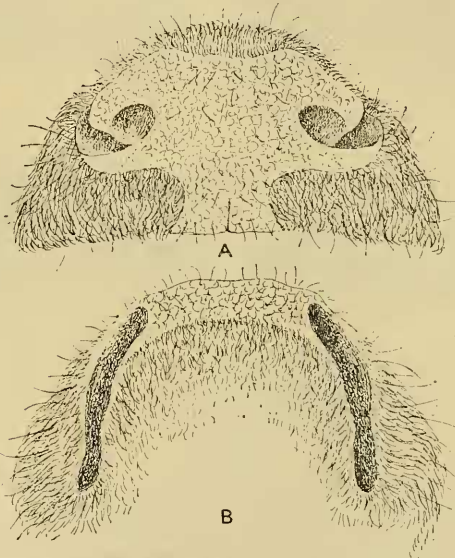
In these two species of *Cervus* the rhinarium is more reduced by hair-growth from the muzzle than in any of the typical deer, except *Dama*, although these genera are surpassed in that respect by *Alces* and *Rangifer*.

CERVUS HORTULORUM Swinh.

As was to be expected, the feet and glands of this species differ in no respect from those of the Japanese species (*Cervus sika*) I described in 1910.

In one example the labial and ocular vibrissæ are normally developed; but the genal and interramal tufts are absent. The rhinarium has a considerable portion of its upper surface, nearly half, overgrown with hairs from the muzzle, which form a convex curve between the nostrils; the infranarial portion is tolerably wide, a little wider than the space between the nostrils. (Text-fig. 3, A.)

Text-figure 2.



A. Rhinarium of Wapiti (*Cervus canadensis*), from the front.
B. The same from above.

Two examples showed an interesting variation in the structure of the penis. In both the urethra was inferior and marked distally by a distinct ridge ending in a slightly upturned point as in other typical Cervine deer; and in one specimen the truncated apex above the urethra was, as usual, lobate, the tips of the lobes folding inwards so as to make a groove where they meet above the point of the urethra. But in the other specimen this terminal portion of the glans was simple and unlobed—a very unusual occurrence. (Text-fig. 17, C, D.)

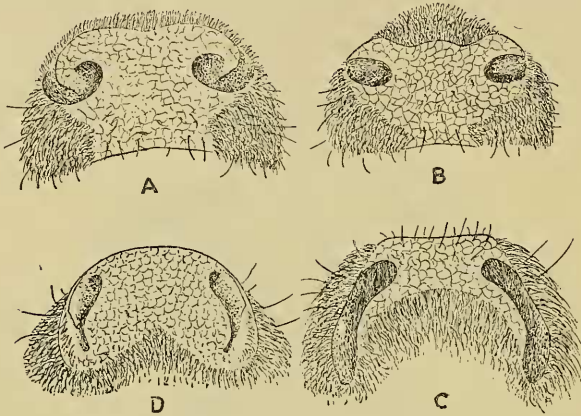
In an example of *C. sika* the glans penis resembled that of the first-described specimen of *C. hortulorum*.

CERVUS ELDI Guthr. (p. 944).

In two additional specimens the feet and glands resembled those of the example described in 1910.

In both specimens the buccal and ocular vibrissæ were well developed. In one of them there was a single long genal and a single long interramal vibrissa. In the other there were two rather widely separated genals, but no interramal*.

Text-figure 3.



- A. Rhinarium of *Cervus hortulorum*, from the front.
 B. The same of *Dama dama*.
 C. The same from above.
 D. The same of *Cervus eldi*.

The rhinarium is large. On its upper side the hair of the muzzle advances in the middle as an angular growth, which reaches to a point approximately in a line with the middle of the nostrils. The infranarial portion is wide, considerably wider than the area between the nostrils. (Text-fig. 3, D.)

Genus AXIS H. Smith.

AXIS AXIS Erxl. and A. PORCINUS Zimm. (pp. 948-950).

Two examples of the Chital or Axis Deer (*A. axis*) examined since 1910 show some interesting variations in the hairiness of the glandular depression on the front of the pastern of the hind foot.

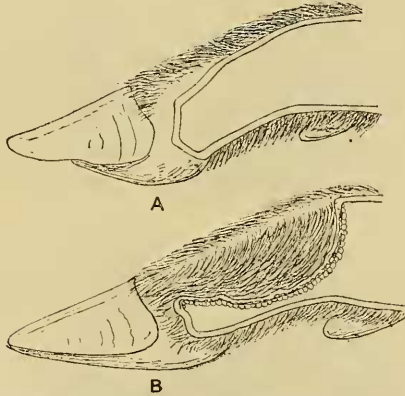
In the specimen originally described the walls of the depression were covered with short, rather sparsely scattered hairs and the

* I have noticed in other species of Cervidæ that the genal and interramal vibrissæ are of inconstant occurrence within specific limits.

interungual tie was naked. In both the other examples the walls of the depression were clothed with long hairs running downwards and forwards, following the curve of the floor of the pouch, but capable of being raised so as to project from its orifice. In one of these two specimens the interungual tie was naked, but in the second it was covered with short hairs. (Text-fig. 4, B.)

One of the interests of these variations is that they break down the differences I recorded in 1910 between the feet of the Chital and of the Hog Deer (*A. porcinus*), in which the interungual tie is hairy and the glandular pouch provided with long projecting hairs. On the strength of these differences I separated *porcinus* from *axis*, retaining for it the subgeneric name *Hyelaphus*; and this opinion was adopted by Lyddeker. Owing to the identity in the structure of the hind foot in the two species,

Text-figure 4.



A. Longitudinal section of the fore foot of *Axis axis*.
 B. The same of the hind foot.

Hyelaphus now falls as a synonym of *Axis* and the latter will contain two species *A. axis* and *A. porcinus*, the genus *Axis* being distinguished from the supposedly allied form *Rusa*, which has similar simple antlers, by the presence of the glandular pouch on the hind foot.

In the two examples of *A. axis* above referred to, the creamy or waxy secretion sticking together the hairs of the glandular pouch smelt like tallow candles, with an admixture of cheese. The fore feet differed in no important respect from those of the specimen described in 1910. (Text-fig. 4, A.)

In a foetal *Axis* Deer, measuring sixteen inches (about 400 mm.) from the snout to the root of the tail and weighing 3 lb., the skin although naked showed faintly all the spots characteristic of the adult. The tail was relatively much longer than in the adult.

The eyes were closed. The only hairs developed were the sensory vibrissæ on the head, the mystacials, submentals, superciliaries, and suboculars being very evident. On the cheek there were two genals and the interramals arose from a warty excrescence. The early development of all the tufts of vibrissæ characteristic of the Mammalia is interesting. The position of the antlers was marked by a depression of the integument on each side of the crown of the head. The preorbital gland was represented by a shallow depression, opening by a short linear orifice a little distance below and in front of the eye. The metatarsal gland was marked by a small pale oval patch on the skin of the leg below the hock. The pedal glands were as in the adult, a deep pit on the hind foot and a shallow pit on the fore foot.

Genus DAMA Frisch.

DAMA DAMA Linn. (p. 950).

The rhinarium in the Fallow-Deer is much reduced by the encroachment of hair from the muzzle and lips. On its upper-side the hair extends nearly as far as the anterior end of the nostrils, leaving only a narrow strip bordering the nostrils laterally above. The infranarial portion is very narrow inferiorly, being at its narrowest point much less than the width of the space between the nostrils. (Text-fig. 3, B, C.)

Genus ELAPHURUS M.-Edw.

ELAPHURUS DAVIDIANUS M.-Edw. (p. 945).

My notes upon this species in 1910 were based upon the observations of others and upon the examination of a dried skin in the British Museum. Since then I have seen two examples in the flesh, both from the Duke of Bedford's herd at Woburn. The first of these, a male, died in the Zoological Gardens from impaction of the psalterium in August 1917; the second, a female, died at Woburn and was kindly sent to me for examination by the Duke in January 1923.

The *facial vibrissæ* are represented by well-developed buccal and orbital bristles; by a small genal tuft on each side below the corner of the eye and above the line of the mouth, and by an interramal tuft of a few short bristles arising from a small elevation. In the male there is an interramal dew-lap which is absent in the female. Perhaps this is seasonally developed.

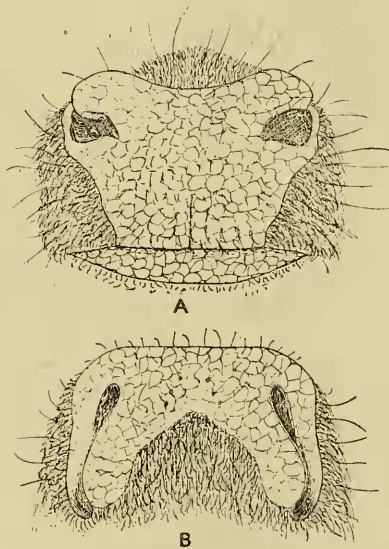
The *rhinarium* is large and naked with the nostrils narrow and widely separated, but with the space between them a little narrower than the infranarial portion, which has a short inferior median sulcus. On the upperside the hair of the muzzle encroaches to a great extent between the nostrils, reaching beyond

the middle of their length, but leaving a wide naked rim above them laterally. Although the rhinarium differs considerably in its nakedness from that of *Cervus canadensis* or *Dama dama*, it is not very unlike that of *Cervus eldi*. (Text-fig. 5, A, B.)

The *preorbital gland* is a deep and long pit, with a naked floor, its orifice when closed being about as long as the eye.

The *ear* is moderately large and thickly clothed with long hairs inside. It has three vertical ridges, the anterior and posterior being stronger than the median. The basal ridge is bilobed, the posterior lobe is much longer than the anterior, but not very much higher, and has a convex edge. Beneath it there

Text-figure 5.



A. Rhinarium and edge of lower lip of *Elaphurus davidianus*,
from the front.
B. Rhinarium of the same from above.

is a curved rounded ridge leading down to the orifice. (Text-fig. 15, A.)

The *feet* are long and broad with the digits widely separable, owing to the shallowness of the interdigital web arising from the depth of the depression between the heels of the hoofs. The upper interdigital depression is approximately as deep as in *Cervus elaphus* or *maral*, and is scantily covered with hairs in its proximal half, naked in the distal half. The hoofs themselves are moderately wide and pointed, but are remarkable for the exceeding length of the heels, which extend backwards almost to

the false hoofs—the latter being exceptionally long, particularly on the fore feet. The area between the false hoofs is naked, except for a narrow strip of hair running on each side from the back of the leg to the heel. The deep depression between the heels is entirely naked. The hind feet differ from the fore feet in being smaller and in having relatively shorter false hoofs. The feet of the female in the winter were more hairy below than those of the male in summer described above. The wide separation of the digits and the length of the heels and of the false hoofs suggest adaptation to swamp-life. (Text-fig. 6, A, B.)

The *metatarsal gland* may, it appears, be present or absent. It is present on the skin in the British Museum; but I could find no trace of it in the female, and have no note on the subject in the male.

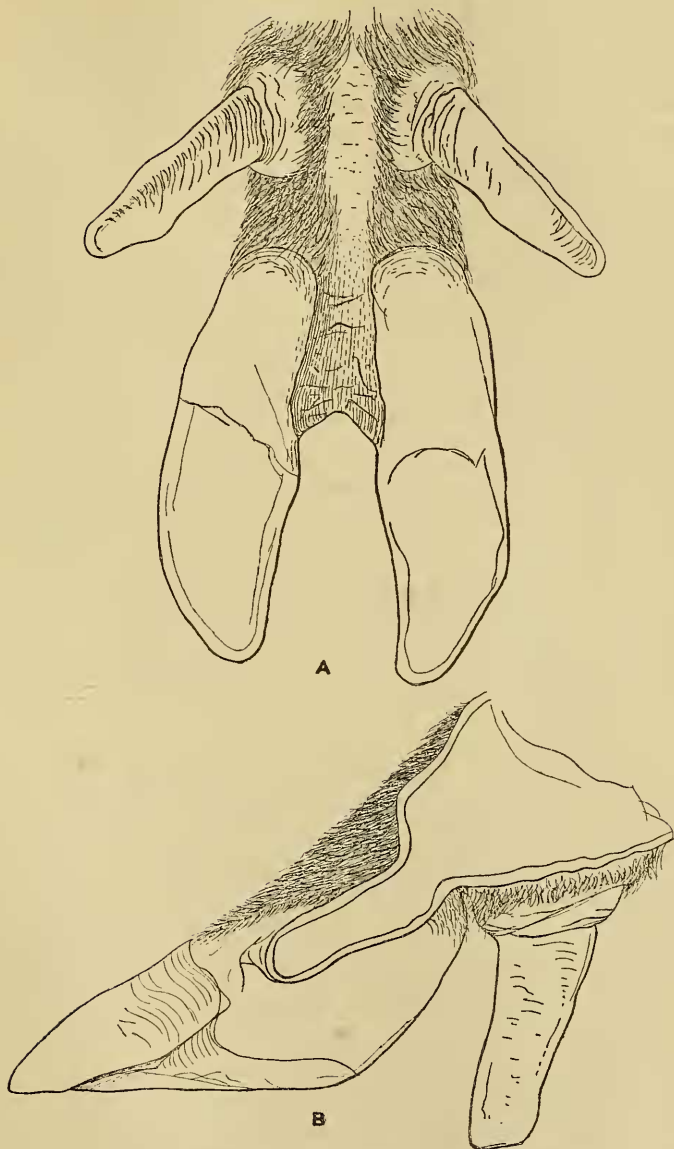
The *penis* is truncated apically and provided with five pairs of lobes which normally fold over the urogenital orifice, but are capable of spreading out like the petals of a flower. Except, however, that the lobes are somewhat better defined, the penis does not differ essentially from that of *Cervus xanthopygus* and of other typical deer of the Old World. (Text-fig. 17, E, F, G.)

It may be recalled that, according to Garrod (P. Z. S. 1877, p. 9), the penis of the American deer now referred to the genera *Odocoileus*, *Mazama*, *Pudu*, and others differs from that of such Old World deer as *Cervus*, *Axis*, *Dama*, etc., in being attenuated at the apex, the urethral canal being produced into a median slender process, unlike the upcurled termination of the urethra, which does not project beyond the truncated tip of the glans in the Old World forms. Hence the discovery of the structure of the penis in *Elaphurus* is the final piece of evidence required to establish the affinity of that genus with the typical Old World deer and to sever it from the American genera with which Lyddeker affiliated it.

Notes on the Seasonal Colour-change and Antler-growth of Elaphurus.

Even as recently as 1915, the colour of *Elaphurus* was described as “reddish tawny with a tinge of grey” by Lyddeker, who judged apparently from the mounted specimen in the British Museum, which was presented to that institution by the Duke of Bedford in July 1899. As a matter of fact, the reddish tint is a transient phase lasting some three or four months of the summer season, roughly from May or June to August or September. For the remaining eight or nine months of the year the animal is the colour of a grey donkey; and this grey coat is thick and luxuriant in the winter, whereas the reddish coat is comparatively short and sparse.

Text-figure 6.



A. Lower side of fore foot of *Elaphurus davidianus*.

B. Section of fore foot of the same.

The stag presented to the Society on January 26th, 1916, by the Duke of Bedford was in the grey pelage. This was replaced by the red pelage in June, and the grey phase was assumed in September and carried through the winter until May 1917, when the red summer coat was substituted. The first clear signs of the shedding of this red coat were noticed on July 23rd. It came away with great rapidity and was all gone in about a week's time, except on the crown of the head, where it persisted until the stag's death in August.

The red phase was therefore about a month earlier in its appearance and disappearance in 1917 than in the previous year.

With regard to the antlers, the stag was carrying a burnished pair on its arrival on January 26th, 1916. These were shed on February 1st. The new antlers grew rapidly and were burnished by the time the grey pelage was replaced by the red pelage in midsummer, when rutting set in. These antlers were shed on October 22nd, and a new pair started at once; but instead of reaching their full size in the winter and being shed in February as in the previous year, they continued to grow through the winter and spring, began to peel in May, coincidentally with the shedding of the grey winter pelage and the appearance of the red summer coat, and were unshed at the time of the stag's death in August. Being the result of about seven months' growth, these antlers were much larger than the preceding pair, which were developed in about four and a half months.

But, as recorded by Lord Tavistock in a letter to me, the antler-shedding in *Elaphurus* is a much more complicated and variable phenomenon than those who have seen single stags are aware. The following is the substance of his observations made upon the herd at Woburn:—

No immature stag grows more than one pair of antlers in a year. The antlers of a yearling are not clean till the end of June and are shed in midwinter or even later. The antlers of a four-year old stag are shed early in November, and may not be clean for three weeks after those of the old stags have lost their velvet. All old stags clean and shed their summer antlers with as little variation as to date as red deer. But the date of the cleaning and shedding of their winter antlers is exceedingly variable. In the case of late shedding of the winter antlers, stags will sometimes be found in May with but very few inches of new velvet-covered antlers; but, no matter how small the growth, these antlers will harden and clean in time for the rutting season. These stumpy-horned stags, however, have very poor chance against their better-armed companions, and it is only when the latter are exhausted at the end of the season that the former have any chance of collecting a harem at all.

Very large antlers of *Elaphurus* are always the result of a winter growth by an adult animal; but the production of a

single pair of antlers of large size instead of two pairs of small or medium size becomes increasingly rare the longer the deer remain in this country. The result is now that the only really handsome heads are those carried by stags five and six years old. As a rule, there is no attempt to resume the rut when the winter antlers harden, the stag remaining as lazy and peaceful as if still in velvet; but one or two stags were known to Lord Tavistock which for several seasons recommenced calling in midwinter. November was the latest month in which he heard stags, still carrying their summer horns, calling; and he has seen a six-year old stag, in full summer coat and carrying a large pair of horns, herding his hinds with great energy and calling in the first week in February. The antlers in this case were the continuous growth of the whole autumn and winter.

The majority of the calves are born in April and May. Very late ones are not common.

In 1922 Ludwig Zukowsky, Hagenbeck's assistant, published a paper* upon *Elaphurus davidianus*, based upon a specimen that was exhibited for nearly two years at Stellingen. Unfortunately, the author was not acquainted with the published literature on this subject. He described in detail the mode of growth of the antlers, and quite correctly spoke of the anterior branch as the "brow-tine." In this he confirmed in every particular my account published in 1912 (P. Z. S. pp. 777-780) from sketches kindly supplied by Lord Tavistock, the accuracy of which I was subsequently able to verify on the specimen exhibited in the Zoological Gardens †. Zukowsky also recorded the succession of the antlers in this aberrant species. The specimen at Stellingen cast its antlers on the following dates:—March 8, 1913, Sept. 18, 1913, March 17, 1914, Oct. 5, 1914, and died on Dec. 30, 1914, with fully developed antlers in velvet.

When Hagenbeck's specimen died it was sent to be mounted to the Natural History Museum, Hamburg, and Herr Gast, Superintendent of that institution, subsequently wrote to Zukowsky to inform him that he had found just beneath the edge of the under lip "a deep sheath or vagina let into the skin, which seemed to point to a glandular duct, one inch in length." I failed to find any trace of this structure in the female specimen of *Elaphurus* which the Duke of Bedford sent to me for the special purpose of investigating this gland. Possibly there may be such a gland restricted to the male; but, so far as is at present known, the cutaneous glands in the Cervidæ are alike in the two sexes ‡.

* I am indebted to the Duke of Bedford for kindly sending me a copy of this paper, which was published in Arch. Naturg. vol. lxxxviii., May 1922.

† When I first suggested in 1910 that the anterior and posterior branches of the antlers of *Elaphurus* are strictly homologous with the "brow-tine" and "beam" respectively of the antlers of ordinary Cervidæ, I was not aware that I had been anticipated in this view by Dr. Theodore Gill, who came to the same conclusion. This was published I believe in 'Forest and Stream,' but I do not recollect the reference.

‡ Following Garrod, I exclude *Moschus* from this family.

Genus HYDROPOTES Swinh.

HYDROPOTES INERMIS Swinh. (p. 956).

Some of the external characters and the visceral anatomy of this aberrant genus were described by Garrod (P. Z. S. 1877, pp. 789-792). Additional information was later supplied by Forbes (P. Z. S. 1882, p. 637).

The head is remarkable for the complete absence of all trace of antlers—a feature in which this genus is unique in the Cervidæ,—the long, slightly curved, pointed and movable upper canines, and the narrow muzzle. (Text-fig. 7.)

The lightly areolated *rhinarium* has a deep wide infranarial portion, which is wider than the supranarial portion and therefore much wider than the internarial area. The latter is of normal

Text-figure 7.

Head of *Hydropotes inermis*.

width. The supranarial portion is unusually high, so that the height of the entire rhinarium, as described by Garrod, is about equal to its width. (Text-fig. 8, C.)

The mystacial *vibrissæ* are tolerably numerous and of average length. The superciliaries and infraorbitals are also normally developed; but in the thick hairs of the cheek and throat I can find no trace of genal or interramal vibrissæ, which are sometimes present but never abundant in other Cervidæ.

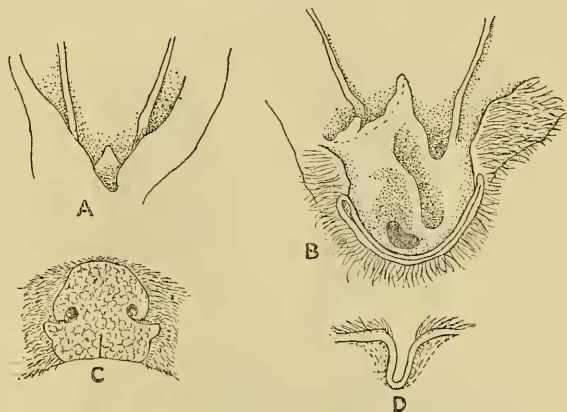
The *preorbital gland* is represented by a small shallow pouch lodged in a naked area of skin just in front of the eye. (Text-figs. 7; 8, D.)

The *ear* is short and broad, and densely clothed within with hairs, which meet in the middle line of the hollow of the pinna.

The overfolded edges of the base of the ear meet at an acute angle. There are two vertical cartilaginous ridges, an anterior and a posterior, supporting the pinna; and the prominences on the basal ridge are very unequal in size, the anterior being quite small and slender, whereas the posterior rises as a high triangular peak. These prominences are quite unlike those of any other species of Cervidæ that I have examined. (Text-fig. 8, A, B.)

Feet.—The hoofs of the fore foot are long and pointed, and tolerably widely separable; the soft inferior cushion, constituting the greater part of the sole, is continued backwards some distance behind the smooth heel-tie which joins the heels together. On the front of the pastern there is a tolerably deep and smooth

Text-figure 8.



- A. Base of ear of *Hydropotes inermis*.
 B. The same cut open.
 C. Rhinarium of the same from the front.
 D. Section of preorbital gland of the same.

glandular depression, and the skin all along the back of the pastern from the heel-tie to the area between and beyond the false hoofs is also glandular. This area is more scantily covered with hair than the area of the leg above the false hoofs, and the false hoofs themselves, which are short, are basally encircled by an area of naked skin divided inferiorly by a narrow scantily hairy strip of skin. (Text-figs. 9, A; 10, A.)

The hind foot is very similar to the front foot, but the hoofs are rather more widely separable, and the heels are narrower and a little longer. As in the front foot the back of the pastern is hairy down to the heels, and the heel-tie is naked. The glandular depression is considerably deeper and longer, and has a more abruptly upturned anterior rim. The widely separable

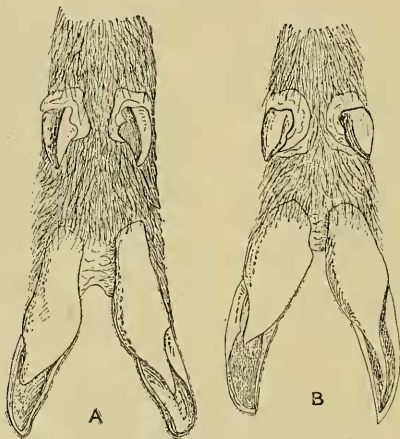
hoofs with their long heels are adapted for progression upon soft marshy ground. (Text-figs. 9, B; 10, B.)

There is no trace of metatarsal or tarsal gland.

The *anus* opens in the upper half of an oval naked area of skin, broader above than below and extending from the root of the tail nearly to the scrotum. The orifice is surrounded by a thickened glandular rim. The edge of the smooth oval area is sharply defined by the thick growth of hair, which is as luxuriant here as elsewhere on the body. The tail is short, only long enough to cover, when depressed, the smooth anal area, and is thickly covered with hair below as well as laterally and above. (Text-fig. 11, B.)

The *inguinal region* has a single pair of teats—not two pairs as recorded by Garrod in the newly-born fawn. The area between them is scantily clothed with long hairs; but on the outer

Text-figure 9.



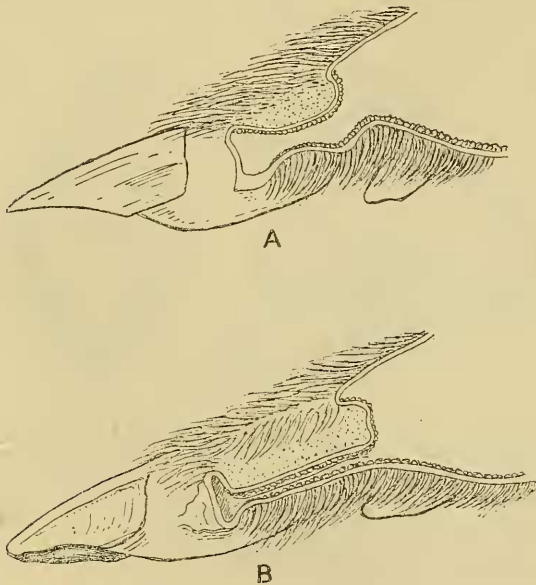
A. Lower side of fore foot of *Hydropotes inermis*.
B. The same of the hind foot.

side of each there is a large nearly naked area of skin extending a considerable distance outwards and backwards; and towards the outer edge of this there is a shallow, curved, glandular depression, recalling the inguinal glands of many of the Bovidae. This is the first record of the presence of inguinal glands in the Cervidae. (Text-fig. 11, A.)

The *prepuce* is a naked button of skin surrounded by long hairs and occupying the normal abdominal position in front of the inguinal region and remote from the scrotum. The *penis* is perfectly simple, straight, and slightly attenuated, with the orifice terminal. It runs between a couple of ridges in the dorsal wall of its sheath. (Text-fig. 11, A.)

The absence of antlers and the presence of large upper canine teeth in *Hydropotes* naturally suggested the possibility of kinship between it and *Moschus*. Since Garrod definitely disposed of this view, it need not be further discussed. He closed his account of the anatomy of *Hydropotes* as follows:—"To what group of the Cervidæ *Hydropotes* is most allied there is still considerable uncertainty. That it is not allied to the New-World type is evident from its vomer not extending downwards to join the osseous palate posteriorly. That it is not Cervuline [related to the Muntjacs, which also have large canines] is equally certain on

Text-figure 10.

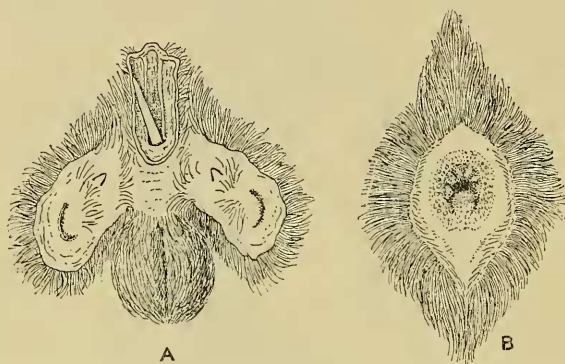


A. Section of fore foot of *Hydropotes inermis*.
 B. The same of the hind foot.

account of its cuneiform bones being free from the naviculocuboids. Its large Spigelian lobe favours the view suggested by Sir Victor Brooke, that it is most closely allied to the Rusine Deer" (p. 792). This view, I think, may be dismissed without hesitation. On the other hand, Forbes's opinion (P. Z. S. 1882, p. 637) that *Hydropotes* is related to *Capreolus* is worth more consideration. The two, at all events, agree in being "telemetacarpalian" and in the structure of the vomer and apparently of the glans penis. But the differences between them are too many and too deep-seated to admit of close affiliation. In the first place, *Hydropotes* is the most primitive of all existing Cervidæ in

the complete absence of the antlers and the presence of long tusk-like canines in the male. *Capreolus*, on the other hand, has well-developed branched antlers, and has normally lost all trace of the canine, being in the latter particular more specialised than *Cervus*. Again, *Capreolus* has lost the preorbital and retained the metatarsal gland. *Hydropotes* has retained the preorbital and lost the metatarsal gland; and has acquired inguinal glands, a new feature in the Cervidæ. The differences between the two in the length and separability of the hoofs are also marked; but, considering the differences of habitat, they are not obviously an indication of remoteness in kinship. The deep and long interdigital glandular depressions in *Hydropotes*, on the contrary, are

Text-figure 11.



- A. Inguinal and genital area of *Hydropotes inermis* ♂, showing the nearly naked area of skin on each side, with a single pair of teats and the shallow pouches of the inguinal glands. The sheath of the glans penis cut open along the middle line, showing the glans turned towards the right and the two ridges forming the groove along which it runs.
- B. Anal area of the same with the tail raised, showing the anus insunk in the surrounding glandular area.

much more primitive than the pouch-like gland of the hind foot of *Cervulus*.

In view of the peculiarities of *Hydropotes*, I propose to separate the genus from the rest of the Cervidæ as the type of a special subfamily, Hydropotinæ.

Genus ODOCOILEUS (= *Dorcelaphus*).

ODOCOILEUS VIRGINIANUS Bodd. (p. 962).

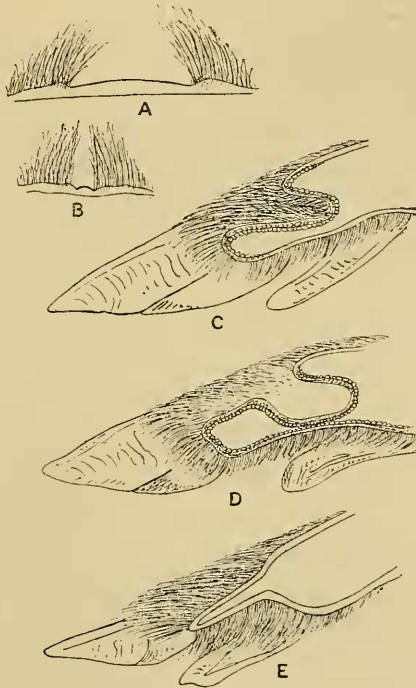
In 1910 I had seen no fresh example of this species, quoted as *Dorcelaphus americanus*, and was only able to describe the glands in the feet, as shown by specimens in the Museum of the College

of Surgeons. Since then I have examined an adult female that died in the Gardens on August 28th, 1911.

The *rhinarium* is large and naked, the hairs of the muzzle encroaching but little on its upper surface; the infranarial portion is wider than the space between the nostrils.

The *preorbital gland* is represented by a very small, shallow pit.

Text-figure 12.



- A. Longitudinal section of the metatarsal gland of *Odocoileus virginianus* (typical form).
 B. Transverse section of the same.
 C. Section of fore foot of *O. virginianus spinosus*.
 D. Section of hind foot of the same.
 E. Section of fore foot of *Moschus moschiferus*.

The *tarsal gland* consists of a patch of thickened vascular skin covered by a thick pad of long hair stuck together with secretion, but without any under-fur; the hairs are umber-brown with white bases.

The metatarsal gland shows externally as an elongated patch of naked, horny, granular skin overlapped by the long, mostly

white hairs growing round it. The secreting glands lie beneath these long hairs, the skin being thicker and more vascular there than elsewhere. The naked area between the long hairs seems to serve as a receptacle for the secretion, since it collects and is encrusted there. (Text-fig. 12, A, B.)

The feet and pedal glands are as described in 1910, except that the pouch on the hind foot is rather more capacious, has a wider orifice and naked walls. The pouch on the fore foot is similar, but only about half the size.

ODOCOILEUS VIRGINIANUS SPINOSUS Gay & Gervais (p. 962).

In 1910 I referred to a living example, identified as *Dorc-elaphus americanus savannarum*, which came from Venezuela and was presented to the Society by Major Albert Pam. The animal died in 1914, and I was able to examine it in a fresh state.

The rhinarium resembles very closely that of the typical North-American form, but from my sketches it seems that the infranarial portion is somewhat narrower inferiorly and the upper surface a little more overgrown with hair in the middle. (Text-fig. 14, A.)

The vibrissæ on the upper and lower lips and above and below the eye are well developed; but there is a single long genal bristle arising beneath the posterior angle of the eye and far back in a line with the mouth. There is no interramal tuft.

The preorbital gland is small as in the typical form.

The tarsal gland is marked by a thickened bunch of hair, brown and white in colour, and covered at the base with secretion.

The metatarsal gland is a very small patch of thickened skin overgrown with white hair.

The glands are well-developed pouches, both on the front and the hind foot. The hind foot hardly differs at all from that of the typical *O. americanus*, the walls of the pouch being naked; but in the fore foot the walls of the pouch are thickly covered with hair and the orifice is much longer than in the typical *O. virginianus*, with the heel-tie shallower. There is also a small naked patch at the posterior inferior angle of the heel-tie. (Text-fig. 12, C, D.)

In this animal, as in the above-described example of the typical *O. virginianus*, the false hoofs of the fore foot are much longer than those of the hind foot.

ODOCOILEUS VIRGINIANUS PERUVIANUS Gray.

A male example from Iquique, presented by Miss Peggy Lomax on April 24 in 1911, died in Jan. 1923 from pneumonia, the worn condition of the teeth showing it to be an old animal. The donor informed me that it was born in 1909. It was therefore

in its fourteenth year. This was the unidentified specimen of *Odocoileus*, of which I described the antler-growth in 1912 (Proc. Zool. Soc. pp. 781-783) to indicate the homology between the so-called "subbasal snag" of the genus *Odocoileus* and the "brow-tine" of *Cervus*.

The description given above of the external characters of *O. v. spinosus* applies very closely to this form. The only variations noted were the presence in *O. v. peruvianus* of a pair of long interramal vibrissæ, of longish hairs on the sides of the glandular pouch of the hind foot, and the reduction in the size of the metatarsal gland. This gland was merely represented superficially by an inconspicuous patch of hairs slightly longer and slightly different in tint from those of the surrounding area of the lower half of the metatarsal area. The skin beneath this felt slightly thicker to the touch, but the only indication of secretion was a small scab on the gland of the right side. This gland was not visible to me in the living animal, and I thought it was absent. It might very easily be overlooked in prepared skins; and this would account for *O. v. peruvianus* having been described as without metatarsal glands. Not improbably they may be sometimes altogether aborted in this subspecies.

The *tarsal gland*, on the contrary, is represented by a large thick mat of longish hairs, which, upon being separated, showed as a mixture of grey and black with yellow secretion at the base.

The *ear* is tolerably large and nearly naked, as in the related race *O. v. gymnotis*. It has two vertical cartilaginous ridges, of which the posterior is much the stronger. Inferiorly it forms the posterior border of a deepish pit, the anterior border of which is a rounded ridge descending from the rounded posterior lobe of the basal ridge. The anterior lobe of this is a little smaller than the posterior; there is a low short longitudinal crest on its outer side, and the anterior vertical ridge terminates on its inner side. A thickened rounded crest, defined in front and behind by a hollow, descends to the bottom of the cavity of the ear and the orifice opens in the anterior hollow. (Text-fig. 15, B.)

The *penis*, as pointed out by Caton for the North-American forms of *Odocoileus*, was pendulous from a point just in front of the scrotum. The tip of the prepuce was almost naked, but just within its orifice were some hairs arising from definite papillæ. The glans, as in other American deer examined, agrees exactly with Garrod's description, ending in a narrowed point with terminal orifice. (Text-fig. 17, A, B.)

Within the limits of the genus *Odocoileus* the preorbital gland and the pedal glands appear to be always present, the latter occurring on both hind and front feet. According to Caton, they are, however, relatively smaller in *O. hemionus* than in *O. virginianus*, *O. columbianus* coming between the two in this particular.

The metatarsal and tarsal glands are variable. The former attains its maximum in development in *O. hemionus*, where, according to Caton, the bare patch of skin overlapped by long hairs may be five or six inches long. In North American examples of *O. virginianus* it varies from less than one inch to an inch and a half in length, whereas in some of the southern forms (such as *O. v. toltecus*, *acapulcensis*, etc.) it is absent. The tarsal gland varies in size and colour according to the species; but I do not know whether it is absent or not. According to Caton, its hairs expand under excitement, like the hairs of the tail and rump, in the North American species.

Genus MAZAMA Raf. (p. 962).

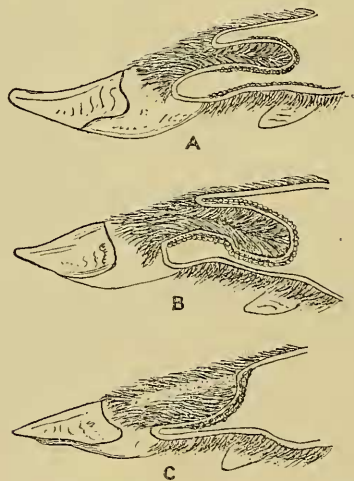
The two species of this genus previously described were *M. nemorivagus* (p. 962) and *M. bricenii* (p. 964).

MAZAMA TEMA Raf.

A single male example from Guatemala, which died on April 26th, 1914.

The *rhinarium* is naked above almost as far back as the

Text-figure 13.



- A. Longitudinal section of the fore foot of *Mazama tema*.
 B. The same of the hind foot.
 C. The same of the hind foot of *Pudu pudu*.

posterior angles of the nostrils and the infranarial portion is very wide, showing laterally as far back as the middle of the nostrils, as in *M. nemorivagus*. (Text-fig. 14, C.)

The normal labial and ocular *vibrissæ* are present; the genal tuft is represented by two bristles beneath the posterior corner of the eye and as low as the line of the mouth; the interramal tuft is composed of three bristles a little behind a line joining the corners of the mouth.

The *preorbital gland* is a small shallow depression, as in *M. nemorivagus* and *M. bricenii*.

The *tarsal gland* is represented by a small tuft of hair, as in *M. nemorivagus*.

The *metatarsal gland* is absent as in *M. nemorivagus* and *M. bricenii*.

The *pedal glands* on the fore foot are much larger and deeper than in *M. nemorivagus* and *M. bricenii*, resembling those of *O. virginianus spinosus* in depth, but having a shorter orifice. The walls are thickly hairy. The heel-tie also is lower than in the other species of *Mazama* and is altogether naked, and the heels of the feet are long and the hoof moderately so. (Text-fig. 13, A.)

The pouch on the hind foot is larger than on the fore foot and has thickly hairy walls as in *M. bricenii*. In this foot also the heel-tie is naked, the heel is long, but the hoof is short. (Text-fig. 13, B.)

This species differs from the other two species of *Mazama* in the large size of the gland of the fore foot. The nakedness of the heel-ties on both fore and hind feet is a character unrecorded elsewhere in the Telemetacarpalian deer.

Genus PUDU Gray.

PUDU PUDU Mol. (p. 967).

The head of this species is remarkable for the forward growth of the hair from between the ears to the summit of the crown, where it meets and forms a crest with the backwardly growing hair of the muzzle and forehead.

The *rhinarium* is tolerably large and lightly areolated; the supranarial portion is mostly naked above, the hair only encroaching upon it to a slight extent posteriorly; the infranarial portion is mesially grooved; it is narrower than the supranarial portion, but a little wider than the space between the tolerably widely separated nostrils. (Text-fig. 14, B.)

The *facial vibrissæ* are represented by some shorter mystacial and submental and longer superciliary and subocular bristles, there being no trace of genal or interramal tufts.

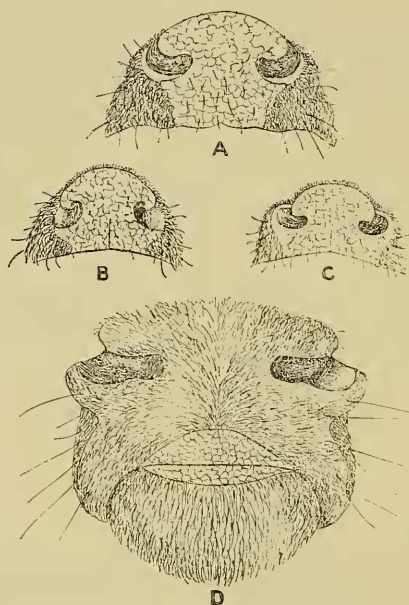
The *preorbital gland* is a comparatively small and shallow pouch, opening on a naked area a little in front of the eye.

The *ears* are rounded, the expanded portion being supported by

four vertical ridges; the basal internal ridge has an angular prominence, which is as high as its posterior rounded termination. (Text-fig. 16, D.)

The *feet* have pointed hoofs with a tolerably short heel and short false hoofs. On the hind foot there is a deep and long interdigital glandular depression, the integument of its floor being almost in contact with that of the back of the pastern. The distal or anterior edge of this depression is not elevated, the heel-tie being shallow and smooth. The walls of the depression

Text-figure 14.



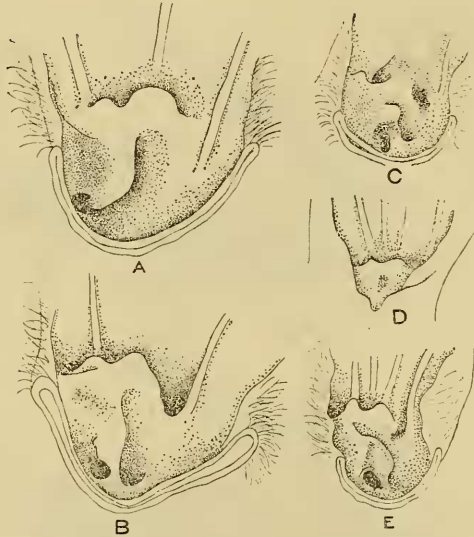
- A. Rhinarium of *Odocoileus virginianus spinosus*, from the front.
- B. The same of *Pudu pudu*.
- C. The same of *Mazama temia*.
- D. The same of *Rangifer tarandus*.

are clothed with hair, which is rusty yellow towards the mouth and white near the bottom. The depression on the fore foot is very similar, but a little shallower. Both tarsal and metatarsal glands are absent. (Text-fig. 13, C.)

In the brief description given by Flower (P. Z. S. 1875, p. 160) of the feet of this species it is said that the pedal glands are not represented by distinct pouches, "but the skin in the depression between the toes . . . is bare and evidently has a free sebaceous

secretion, representing, in the author's opinion, the most rudimentary or earliest stage of an interdigital gland." How little this account accords with the actual facts may be seen by comparing it with the description given above. I was completely misled by Flower into imagining that the interdigital areas in the Pudu resemble those of *Cervus*, surprising as such a conclusion was. There is in reality no such resemblance. The depressions are like those of the hind foot of the Fallow-Deer (*Dama dama*) and of the Muntjacs (*Muntiacus = Cervulus*) and *Elaphodus*, which I described and figured in 1910: that is to say, they

Text-figure 15.



- A. Base of ear of *Elaphurus davidianus*, cut open.
 B. The same of *Odocoileus virginianus peruvianus*.
 C. The same of *Tragulus*.
 D. The same of *Pudu pudu*.
 E. The same of *Muntiacus muntjak*.

belong to what I believe to be the most primitive type of pedal gland in the Cervidæ—a long deep depression the floor of which is in contact, or nearly so, with the integument of the back of the pastern. No other genus of Cervidæ inhabiting America has feet of this type, so far as is known. *Cervus canadensis* may be set aside as an alien from Asia; but in *Rangifer*, *Odocoileus*, and *Mazama* the glandular depression of the hind foot is a deep pouch with constricted orifice, whereas in the front foot it is a small shallow pit, the heel-tie in both cases being deep.

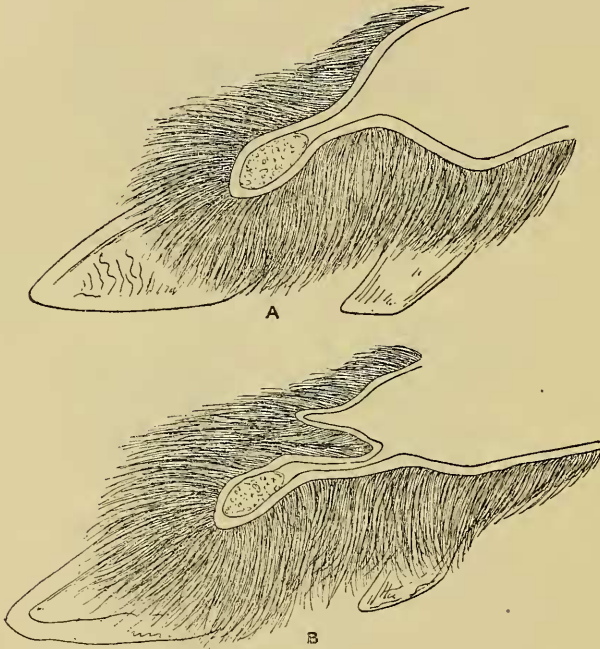
Genus RANGIFER H. Smith.

RANGIFER TARANDUS Linn. (p. 960).

In 1910 I was only able to examine the dried limbs of the North American race of this species, *R. tarandus caribou*. That account I can now supplement by observations upon a female specimen that died in the Gardens on July 27th.

The muzzle of the Reindeer has been described as covered with hair, as if there was no trace of rhinarium. It is true that the

Text-figure 16.



A. Section of fore foot of *Rangifer tarandus*.
 B. The same of hind foot.

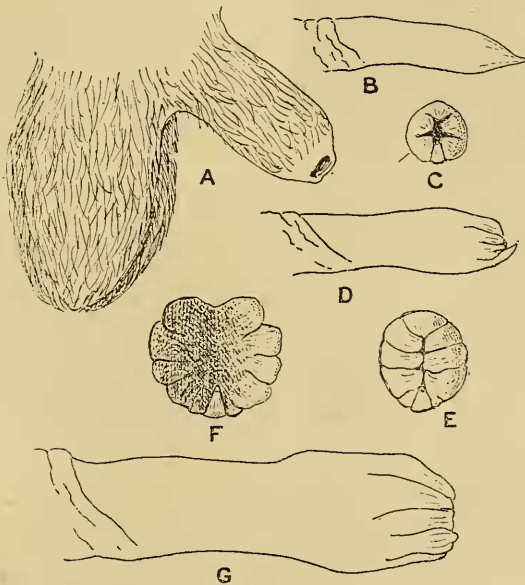
area above, between, and below the fleshy valvular nostrils is entirely overgrown with short soft hair; but along the edge of the upper lip there is a naked areolated tract, wider than the space between the nostrils, with convex upper edge and similar in sculpture and width to the corresponding tract on the edge of the lower lip, but about twice as deep. (Text-fig. 14, D.)

This is the inferior portion of the rhinarium retained. In this particular the Reindeer is unique amongst the Cervidæ.

The external appearance of the well-developed tarsal gland was fully described by Caton, and I have nothing to add to his description or to my account of it published in 1910. The metatarsal gland, as Caton and others have stated, is absent.

My first account of the feet, taken from dried specimens, requires some modification. On the fore foot of the fresh specimen there is a deeper depression on the front of the pastern; and on the

Text-figure 17.



- A. Penis and scrotum of *Odocoileus virginianus peruvianus*, showing the long pendulous prepuce close to the scrotum.
 B. Glans penis of the same.
 C. Apex of glans penis of *Cervus (Sika) hortulorum*, from the front.
 D. Glans penis of the same from the side.
 E. Apex of glans penis of *Elaphurus davidianus*, with lobes folded, from the front.
 F. The same with lobes expanded.
 G. Glans penis of the same from the side.

back of the pastern the depression is deeper still, the integument forming the floor of the posterior depression being almost in contact with that of the anterior depression, so that the two digits are joined together by a very shallow fold or loop of integument. This loop expands towards the hoofs, and the expanded portion is filled with a mass of soft, fatty, somewhat gelatinous material. But there is no trace of a glandular pouch

on the fore foot*. It is to the remarkable shallowness of the integumental fold between the digits and the depth of the depression on the back of the pastern that the wide separability of the hoofs in *Rangifer* is due. The skin of the interdigital depressions is everywhere covered with long thick hair. In the hind foot, the posterior depression of the pastern is not so deep as on the fore foot, but the integumental fold is very similar, although even shallower proximally. On the front of the pastern the depression is deeper and forms a deep glandular pocket very like that of *Odocoileus*. (Text-fig. 16, A, B.)

A species which even surpasses *Rangifer* in the extreme shallowness of the heel-tie and the depth of the depressions between the digits is the Musk-Deer (*Moschus*), which has the hoofs similarly separable for progression on soft snow and for the sure-footed descent of steep slopes. (Text-fig. 12, E.)

Classification of the Cervidæ.

In 1910 I divided the Cervidæ into two subfamilies, Capreolinae and Cervinae, corresponding respectively to Sir Victor Brooke's divisions Telemetacarpalia and Plesiometacarpalia. It appears to me that we must adopt Brooke's primary grouping of the family; but that the genera of both groups, more particularly of the Telemetacarpalia, are too diversified to be assigned to the two subfamilies proposed. It may be claimed at all events, I think, that the subfamilies tabulated below are as well defined as the subfamilies of the Bovidæ:—

- | | |
|---|----------------------|
| a. Distal ends of lateral metacarpals retained, proximal end aborted (Telemetacarpalia). | |
| b. Vomer dividing the posterior nares. | |
| c. Naviculo-cuboid and external cuneiform bones of tarsus united; pedal glands a deep long cleft, with shallow heel-tie..... | <i>Pudinae.</i> |
| c'. Naviculo-cuboid and external cuneiform bones separated; feet with pouch-like pedal glands and deep heel-tie. | |
| d. Antlers present in males only; prepuce long, scrotal in position; feet compact, tightly tied at the heels; rhinarium large and normal..... | <i>Odocoileinae.</i> |
| d'. Antlers in both sexes; prepuce short, abdominal; feet widely separated at the heels; only the labial portion of the rhinarium retained..... | <i>Rangiferinae.</i> |
| b'. Vomer not dividing the posterior nares. | |
| e. Antlers absent, male with large upper canine tusks; inguinal glands present; tarsal and metatarsal glands absent; pedal glands deep long clefts..... | <i>Hydropotinae.</i> |
| e'. Antlers present in males; upper canine teeth absent or minute; no inguinal glands; tarsal or metatarsal glands present; pedal glands a deeper shallow pouch on hind foot. | |

* Caton put on record the very interesting fact that in reindeer calves there are traces of a glandular pouch on the fore foot. This suggests that the pedal glands in *Rangifer* were originally present on both fore and hind feet, as they are in *Odocoileus*.

- f. Muzzle short, not swollen; rhinarium large and normal; preorbital and tarsal glands absent, etc. *Capreolinæ.*
- f'. Muzzle very long and much swollen; rhinarium reduced to a small triangular patch between the anterior ends of the nostrils; preorbital and tarsal glands present, etc. ... *Alcinæ.*
- a'. Distal ends of lateral metacarpals lost, their proximal ends usually retained, rarely vestigial or absent (Plesiometacarpalia).
- g. Naviculo-cuboid and external and median cuneiform bones of the tarsus fused into a single bone. Large upper canine tusks present in males; antlers supported on a long hairy pedicel... *Muntiacinæ.*
- g'. Naviculo-cuboid and cuneiform bones separated. Upper canines small or absent; antlers supported on a short pedicel. *Cervinæ.*

Many of the subfamilies mentioned above—namely, Rangiferinæ, Hydropotinæ, Capreolinæ, and Alcinæ—are monotypical.

The Pudinæ contains the two genera *Pudu* and *Pudella*, the latter differing from the former in the loss of the preorbital gland and the lacrymal pits, and in having the first lower incisor much larger than the second.

To the Odocoileinæ I refer, in addition to the typical genus, *Mazama*, *Hippocamelus*, and *Blastocerus*, although the inguinal position of the prepuce and the structure of the feet are unknown in these three. If one or more of them prove to have the prepuce abdominal, I should separate such forms as a distinct subfamily on that character alone.

The Muntiacinæ* contain three genera—*Muntiacus* (= *Cervulus*), *Procops* †, nov., and *Elaphodus*. The type of the new genus *Procops* is *Cervulus fœæ*, Thomas & Doria, which is generically separated from *Muntiacus* by the absence of the frontal glands, a character in which it resembles *Elaphodus*.

The Cervinæ, containing most of the Old World deer, are a highly diversified group, composed of the following well-defined genera:—*Dama*, *Axis* (+ *Hyelaphus*), *Cervus*, and *Elaphurus*. But *Cervus* itself is subdivisible into several minor groups—*Rusa*, *Sika*, *Rucervus*, and *Cervus* itself—which in the future will probably take full generic rank.

* Established by Garrod under the name *Cervulinæ* (P. Z. S. 1876, p. 757), based on *Cervulus*, which is antedated by *Muntiacus* now in general use.

† From *Prox*, a generic name applied by Ogilby to the Muntjacs.